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Report

Vervet Monkeys Solve a Multiplayer "Forbidden Circle Game" by Queuing to Learn Restraint

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Summary

In social dilemmas, the ability of individuals to coordinate their actions is crucial to reach group optima [1]. Unless exacted by power or force, coordination in humans relies on a common understanding of the problem [2], which is greatly facilitated by communication [3, 4]. The lack of means of consultation about the nature of the problem and how to solve it may explain why multiagent coordination in nonhuman vertebrates has commonly been observed only when multiple individuals react instantaneously to a single stimulus, either natural or experimentally simulated [5, 6], for example a predator [7, 8], a prey [9, 10], or a neighboring group [11–14]. Here we report how vervet monkeys solved an experimentally induced coordination problem. In each of three groups, we trained a low-ranking female, the "provider," to open a container holding a large amount of food, which the providers only opened when all individuals dominant to them ("dominants") stayed outside an imaginary "forbidden circle" around it. Without any human guidance, the dominants learned restraint one by one, in hierarchical order from high to low. Once all dominants showed restraint immediately at the start of the trial, the providers opened the container almost instantly, saving all individuals opportunity costs due to lost foraging time. Solving this game required trial-and-error learning based on individual feedback from the provider to each dominant, and all dominants being patient enough to wait outside the circle while others learned restraint. Communication, social learning, and policing by high-ranking animals played no perceptible role.

Results

The Provider's Dread of Having Dominants Close by Creates a "Forbidden Circle"

The experiment with the captive Strasbourg group ran from March to September 2004 and consisted of 44 trials during which the provider could once per trial open her container filled with about 1 kg of small pieces of canned peaches or apricots and dried figs. The two wild groups, Donga and Picnic, were studied in Loskop Dam Nature Reserve, South Africa. We conducted 40 trials, which correspond to the "single provider" trials of the biological market experiment we reported previously [15], in two blocks: 24 trials from October 2005 to January 2006, and 16 trials from May to June 2006. Here the reward consisted of 120 small pieces of apple (about 750 g), but in order to reduce pressure on the provider, we threw 48 extra pieces 3–5 m from the container after the provider opened it during a first block of 24 trials. We did this to enlarge the food patch, fearing that otherwise there would be too much pressure on the provider, which could discourage her from approaching the container in later trials. In hindsight, this fear was unfounded in the case of the Donga group, but the provider of the Picnic group was indeed attacked by the highest-ranking female (F2) just before we could provide the extra apples in the first two trials. The extra apples were mainly consumed by low-ranking animals and had little effect on the amounts consumed by the dominants. We therefore had no reason to expect, nor did we see any indications, that the extra apples changed the behavior of the dominants before the opening of the box in any way. No trial ended before the provider had touched the container, so we only had to reward her for touching the lid at first and subsequently for touching a red paint mark by opening the container using our remote control, a classical training method known as "shaping" [16]. The training of the three providers took only a few trials each.

The reward never lasted longer than 3 min (range 66–178 s) after the opening of the container. Vervet monkeys have cheek pouches in which they can tuck away pieces of fruit as fast as their hands can grab it. This means that delays measured in seconds were significant in the scramble competition for the reward. High-ranking animals could claim the best spots but rarely gained a competitive advantage through overt aggression. Dominants concentrated on grabbing pieces of fruit for themselves rather than chasing others away, which would only have freed the way for third parties. Thus, although the quantity of the reward was such that most animals had a good chance of obtaining some fruit in each trial and remained interested in the reward, a combination of arrival order and rank determined the portion each individual got.

The rank orders of all three groups were linear, and there were eight individuals dominant to the provider in Strasbourg, five in Donga, and three in Picnic (Table 1). None of the three providers approached the container unless all dominants were roughly 10 m or more away from it, but they did so quickly once the dominants were all sufficiently far away (Figure 1). A distance of 10 m gave a head start to the provider that might seem slight, but the median time that the dominants needed to cover 10 m was about 6 s (range 4–15 s), which was worth about five pieces of fruit to the provider. The dominants often climbed a tree just outside the forbidden circle to keep an eye on the container and so lost a few extra seconds by having to climb down first (see Figure S2 available online). The three providers did not tolerate each dominant at exactly the same minimum distance. In general, the more powerful the dominant was relative to the provider, the greater the minimum distance at which the provider tolerated the dominant. The distance to the container is, in fact, a proxy for the time it takes to

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Table 1. Dominance Hierarchy of the Adult Members in the Three Groups

Strasbourg	M1 – M2 – F3 – F4 – F5 – F6 – F7 – F8 – F9* – M10 – F11 – F12
Donga	M1 – F2 – F3 – F4 – F5 – F6* – M7 – M8 – F9 – F10
Picnic	M1 – F2 – M3 – F4* – M5 – F6 – F7

M = male; F = female. Numbers indicate rank, with 1 = highest rank. Asterisks indicate providers. For tests of linearity and steepness, see Supplemental Results.

reach the container, and we assume that the provider estimated the time it would take a particular dominant to reach the container from a particular location. The "forbidden circle" that we refer to is therefore in reality a collection of frayed circles with diameters somewhere between 10 and 15 m rather than a single neat circle with a 10 m radius. Our game theoretical analysis of the experiment allows for individual-specific minimal distances, as long as these differences are not too large.

The Learning Process of the Dominants: Individually, Fast, and Down the Hierarchy

In contrast to standard coordination experiments with both humans and nonhumans, and more in line with naturally occurring problems, at the time the experiment started no vervet knew that the provider could unlock the food container. Furthermore, all had to learn that she approached the container only if all those dominant to her stayed sufficiently far away. The food was so attractive, however, that all vervets had a natural inclination to guard and monopolize the container. From each dominant's viewpoint, and before learning more about the provider's role and preferences, there was a choice between controlling a rich prize and leaving it up for grabs for other members of the group. By approaching and guarding the closed container, a dominant thus acted out of (mistaken) self-interest and harmed the group's public interest. For the coordination problem to be solved, it was thus necessary that all dominants learn to avoid this tempting strategy and keep the distance the provider required.

Figure 2 gives the cumulative number of minutes that each dominant was at less than 10 m from the container over the series of trials. Following common practice in learning research, we calculated the best-fitting Weibull function [17]. After verifying the close fit with the empirical data, we calculated breakpoint values to determine the trial at which the behavior of each dominant showed a significant change (details in Supplemental Results). Figures 2 and 3 show that the animals learned sequentially rather than simultaneously. For both Strasbourg and Donga, the learning order correlated closely with the rank order (Spearman tests; Strasbourg: $n = 8$, $\rho = 0.98$, $p < 0.001$; Donga: $n = 5$, $\rho = 0.98$, $p = 0.05$). In Picnic, the three dominants showed restraint in the order 2^{nd} in rank (alpha female) > 1^{st} (alpha male) > 3^{rd} (beta male). Once all dominants had learned to stay out of the forbidden circle from the start, there was no relapse. From that trial onward, no dominant came close to the container before it was opened, not even after a break of more than six months (208 days for Donga; 195 days for Picnic), between the two trial blocks in the Loskop groups (Figures 2 and 3). The dominants thus learned one after the other and, with few exceptions, in hierarchical order from high to low. The steep ascent in the Weibull curves (Figure 2) indicates that most animals needed only a few trials to learn self-restraint, but there was little evidence for systematic single-trial learning.

The "Forbidden Circle Game"

We offer a post hoc analysis of a stylized "Forbidden Circle game" in which all dominants are assumed to choose their position relative to the container independently of each other on the basis of cues each of them has received from the provider. All dominants act as players that each individually have an incentive to remain close to the center of a circle but, in order to obtain a share of a communal reward, have to learn to leave it simultaneously. A single player lingering in the circle prevents all players from obtaining any reward, making this player comparable to the weakest link in a chain. A similar "weakest link coordination problem" confronts groups of diners that go hungry while waiting for the last person to show up before being seated [18]. Note that "coordination" refers to an observed outcome of behavioral choices, such as waiting patiently for others to learn, and not to attempts to "coordinate" with others. Also, the Forbidden Circle game is used as a model of a coordination problem but is not a standard coordination game with multiple Nash equilibria.

We first describe the game structure as external observers who are completely informed about the role of the provider and about her reluctance to open the container with dominants nearby. We then take the viewpoint of a dominant with incomplete information and see how his or her assessment of the payoffs is likely to evolve while learning about the role of the provider and her reaction to dominants. How agents figure out which game they are playing is considered to be an important but understudied question [18, 19]. Most multiagent experimental games played in laboratories also require novel behavior, but both human [18] and animal [20, 21] participants usually learn the rules, possible actions, and payoffs through training or instruction, and their grasp of the game is verified before the actual experiments start. In real life, however, players are often confronted with unfamiliar situations in which it is not obvious that coordination yields higher payoffs than the pursuit of private gains. The present coordination problem therefore is a much more natural challenge than most experimental coordination problems reported so far, even though the provider's privileged role was created experimentally.

The players have three possible actions to choose from: *G* (guarding the container and/or trying to open it), *W* (watching the container from outside the forbidden circle), and *R* (roaming, which allows foraging, social interactions, and so forth but prevents monitoring the container). At the moment of opening, action *W* yields a higher payoff than action *R*, independent of the rank of the player. When all players are completely informed and rational, they should leave the forbidden circle as soon as the trial starts but remain as close to the container as the provider allows, i.e., wait just outside the forbidden circle. This is the unique undominated Nash equilibrium of the game with full information. The animals do not have essential pieces of information, however, and can only acquire these by learning. Approaching and trying to guard the still closed container, the "myopic" action *G*, is the natural initial choice, as we could observe (Figure 3). All *G* and *W* players pay opportunity costs due to lost roaming time as long as at least one player chooses action *G*. *R* players do not pay these opportunity costs, but the longer the opening is delayed, the more food depletion in the vicinity of the container reduces their feeding rate, pushing them away from the container. As long as the opening of the container is delayed long enough to make the value of roaming offset the advantage of arriving early, action *R* yields higher payoff than action *W*; hence, learning individuals should switch from *G* to *R*. The more dominants learn to

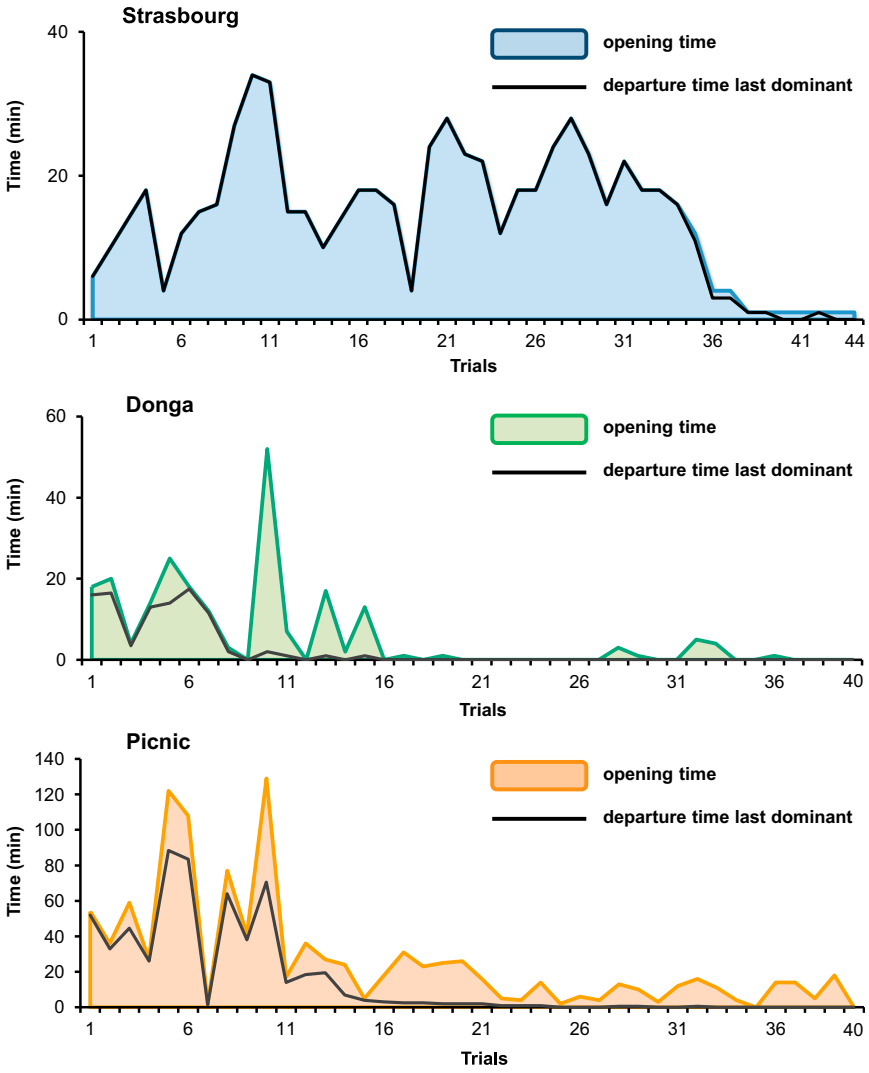

Figure 1. Correlations between the Time Dominants Went beyond the Critical Distance and the Moment the Provider Opened the Container

x axis represents trial number; y axis represents time elapsed after start of trial. The black line represents the time the last animal dominant to the provider left the 10 m radius circle around the container. The filled colored line represents the time the container was opened. Spearman rank correlations between "forbidden circle left" and "container opened": Strasbourg: $\rho = 0.999$, $p < 0.01$; Donga: $\rho = 0.830$, $p < 0.01$; Picnic: $\rho = 0.837$, $p < 0.01$.

show restraint, the shorter the time until the provider arrives and, with short opening times, it becomes optimal for players to switch from *R* to *W*. Our game theoretic analysis indicates that this switching will be in hierarchical order, from high to low, with players ultimately reaching the Nash equilibrium (see Supplemental Game Theoretic Analysis for a detailed analysis of the game).

Discussion

Alternative Solutions that Were Not Used

An appreciation of the reaction of the provider to the behavior of other dominants would have allowed faster learning by imitation, or eventually emulation [22], of the other dominants' behavior. After the animal at the head of the queue, henceforth called "Alpha," learned restraint, all the others could in principle have imitated Alpha's behavior and eventually become an imitated model in turn. In that case, we should have seen all dominants ranking below Alpha showing restraint more or less simultaneously within the next few trials, unless each individual would have needed one or more direct interactions with the provider to test whether the latter indeed reacted as anticipated. Yet, any form of social learning should have led to an acceleration of the learning process further down the queue, but this is not obvious from our data (Figure 3). The time lapse between two dominants learning restraint was not noticeably shorter further down the learning queue in the two larger groups (Figures 2 and 3). Our results do not allow us to categorically exclude that the animals benefited from some social learning, however.

The ability to project oneself in the role of another interacting with a third party, which would imply having at least some degree of "theory of mind" [23], would also have allowed high-ranking dominants to punish [24] lower-ranking ones for not leaving the forbidden circle, i.e., to solve the problem by policing [25]. We never observed behavior by dominants that could be interpreted as preventing lower-ranking dominants from entering the forbidden circle, however. Vervets probably have the required knowledge of the dominance relationships of their group members [26], but whether monkeys possess the cognitive capacities for perspective taking in the context of social interactions is hotly debated [27]. Policing several group members remotely would also have been difficult for an animal that had to keep his distance himself.

Individual Reinforcement in the Learning Queue

A dominant's learning process could start only after all other dominants waiting near the container gave up and left the forbidden circle to pursue other activities or, in game parlance, switched from *G* to *R*. Only then could onlookers see how the provider opened the container that they could not open themselves. In Strasbourg and Donga, all dominants gave up their attempts to monopolize the closed container after the first few trials. In Picnic, however, a group that regularly raided garbage bins and occasionally took food from tourists, the highest-ranking female (F2, the one that also attacked the provider) guarded the container from the start of the trial for up to 88 min during the first six trials.

To avoid being the weakest link, each dominant had to learn how his or her own guarding behavior influenced the behavior of the provider. The higher its rank, the sooner the animal was likely to learn restraint. This does not necessarily point to superior cognitive abilities but can be explained by priority of

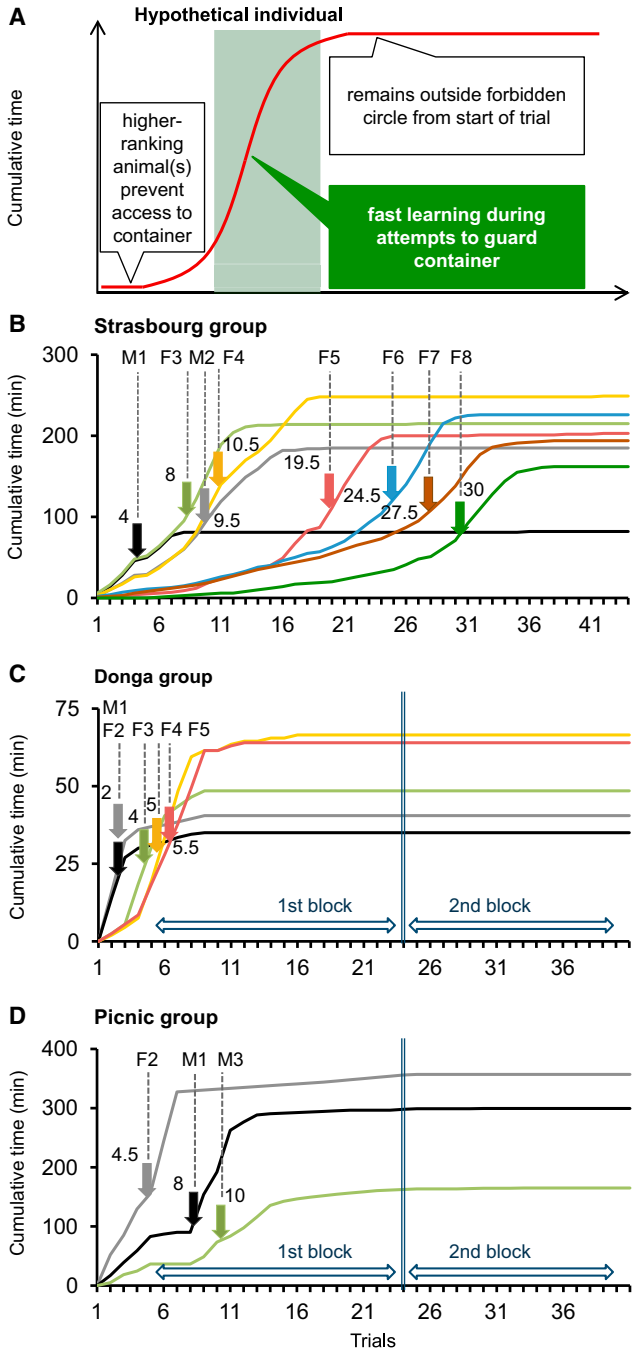

Figure 2. Cumulative Individual Learning Curves

Cumulative time elapsed before each animal left the forbidden circle. The idealized curve of a hypothetical dominant is shown in (A). These leaving curves are closely correlated to the Weibull curves designated by the function $R = A(1-2)^{-(x/L)^s}$, where R is the cumulative retreat time; A is the asymptotic level (reached when the animal consistently shows restraint from the start of the trial); L (indicated by arrows) is the breakpoint (trial corresponding with $A/2$), the first trial after which the animal left the forbidden circle significantly faster than before; and s describes the steepness of the slope. Average z values of Kolmogorov-Smirnov goodness-of-fit tests between empirically observed and Weibull curves were 2.158 (Strasbourg), 3.419 (Donga), and 2.314 (Picnic). The vertical lines in (C) and (D) indicate a break of >6 months between two series of trials in the Loskop groups. M = male; F = female; numbers indicate rank, with 1 = highest rank.

access to learning opportunities. That high-ranking animals learn first, because they have priority of access to the apparatus, has been observed before in experiments in which group-living animals had to solve technical problems (e.g., [28–30]). The accomplishment of our vervets has a different quality, however: They had to motivate a conspecific from a distance to perform the behavior they desired, as opposed to handling an apparatus at close range, and they could never be sure that their personal activities alone caused a specific reaction of the provider. Each animal would have had little opportunity to see an effect directly related to its own moves, when the provider would have stayed at more or less the same distance from the container until all individuals ranking above her would have learned to stay away. Most dominants could observe a faster approach by the provider when they retreated earlier from the forbidden circle, as shown in Figure 3. This effect lasted only a few trials, until the next in line began to block the provider, but may have served as a crucial reinforcement stimulating the dominant's faster departure.

Patience and Cheek Pouches: Essential Ingredients of the Solution

The point at which all players simultaneously showed restraint would never have been reached without the remarkable patience shown by the animals at the head of the learning queue. Notably, in Strasbourg the queue was rather long, and it took 30 trials before all eight dominants stayed outside the circle simultaneously from the start. We see two nonexclusive explanations for this forbearing attitude: (1) the temporary improvements in opening times also reinforced the behavior of the dominants that had already learned their lesson, and/or (2) the deterioration in the provider's behavior was not perceived as being associated with intrusions by others.

The combination of cheek pouches (which only the members of the cercopithecine family have among primates [31]), patience, strong self-control, and the ability to learn fast was essential for solving this coordination problem. What we did *not* observe is perhaps even more remarkable: neither punishment nor any conspicuous form of communication among the dominants that could have improved their coordination. Nevertheless, multiple vervets managed to show restraint simultaneously, in spite of being attracted to the closed container, allowing the providers to make the food available to all members of their groups.

Experimental Procedures

Study Groups

The Strasbourg group was held in a 0.5 ha densely wooded enclosure in the Centre de Primatologie near Strasbourg, France. The group consisted of 25 individuals belonging to the West African species *Chlorocebus sabeus* [32]: three adult males, eleven adult females (two of which died during the study), and eleven juveniles and infants. The two South African *Chlorocebus pygerythrus* groups had home ranges of about 3 km^2 each that were about 3 km apart in the Loskop Dam Nature Reserve (M'Pumalanga, South Africa) [15, 33]. The Donga group had three adult males, seven adult females, one or two subadult males, and one or two infants; the Picnic group had three adult males, four adult females, one juvenile male, and two to six infants.

Food Provider Experiment

At both study sites, we used identical (apart from details of the remote controls, which were adapted from 12V car door locking mechanisms) 50 × 55 × 15 cm food containers, with wooden frames covered with plastic mesh on all sides and reinforced with a metallic grid on top, allowing the vervets to see and smell the food (Figure S4). In Loskop, we waited until the groups were in a place that was suitable for the trials, an open area surrounded by large trees in which the vervets could rest. We positioned the

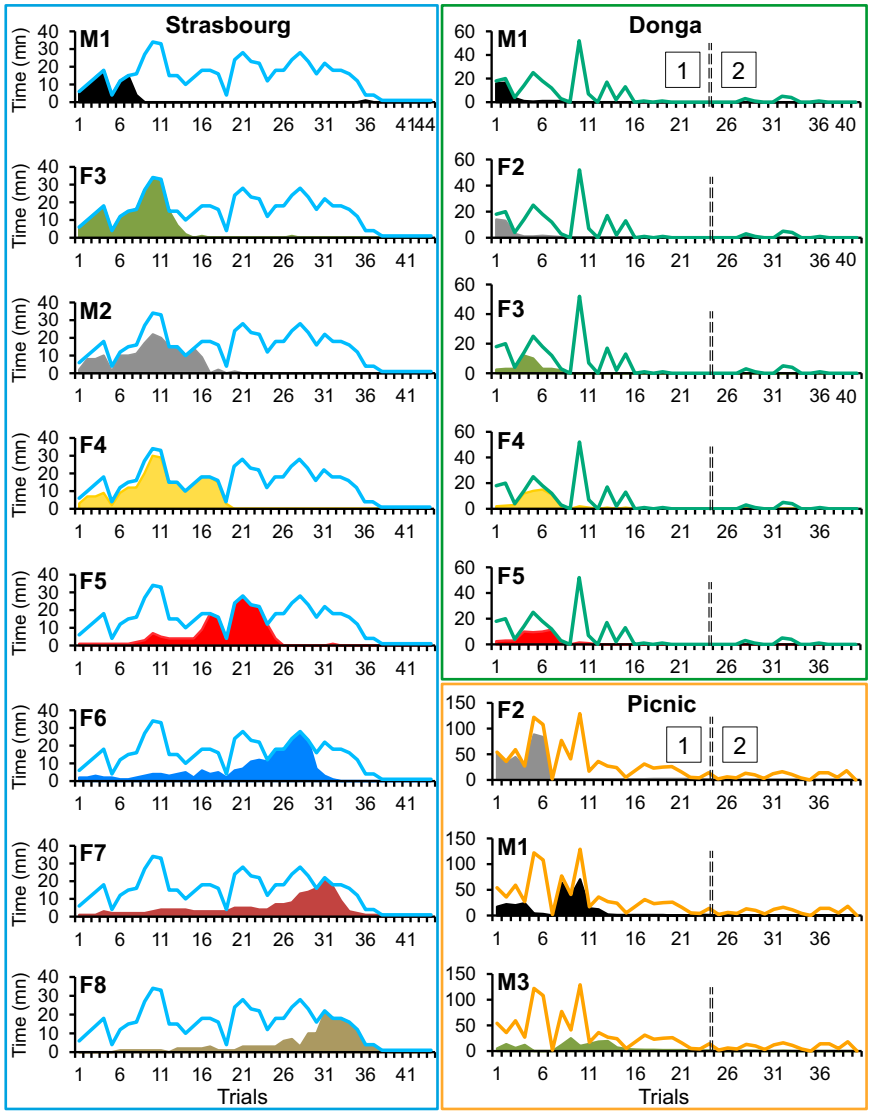

Figure 3. Description of Each Dominant’s Time of Departure from the Forbidden Circle

Lower, filled lines: time needed to leave the forbidden circle per individual. Upper lines: time at which the provider opened the container (blue, Strasbourg; green, Donga; orange, Picnic). For each group, the animals are ordered according to the trial at which they reached their breakpoint *L* (see Figure 2). Note that each time a dominant learned restraint, the provider temporarily took less time, but they relapsed to longer opening times when the next dominant started monopolizing. M = male; F = female; numbers indicate rank, with 1 = highest rank. For the Donga and Picnic groups, the dashed vertical line represents the >6-month break between trial blocks 1 and 2.

video camera and synchronized the recording by means of an acoustic signal that also announced the start of the trial to any animals out of sight of the container. Throughout each trial, the location of all individuals within 20 m of the container was recorded every 30 s. At distances up to 10 m, we estimated the distance to the nearest meter. Beyond 10 m, we used the categories10–15 m, 15–20 m, and >20 m. Individuals that were out of sight, which was never the case within a radius of 10 m around the container, were recorded as “not visible.” The opening of the container was filmed, and providers were observed for the following hour.

Statistical Tests

Two-tailed statistical tests were performed using R (version 2.10.1) [34]. The α level was set at 0.05.

Supplemental Information

Supplemental Information includes Supplemental Results, Supplemental Game Theoretic Analysis, Supplemental Experimental Procedures, five tables, three figures, and one movie and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.02.039.

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